The Proboscis of the Syllidea. Part I. Structure.

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With Plate 15.

I. Divisions of the Proboscis Region.

The proboscis of the Syllidea (here taken as comprising all that part of the digestive tube lying in front of the intestine) is made up of five parts (fig. 6), which are all (with the exceptions presently to be noted) sharply marked off from one another. These will be referred to here as (1) the buccal chamber, (2) the pharynx, (3) the proventriculus, (4) the ventriculus, and (5) the post-ventriculus with a pair of caeca appended to it.

Ehlers (1864) recognized in the region (1) 'Rüsselröhre' (buccal cavity), (2) 'Schlundröhre' (pharynx), (3) 'Drüsenmagen' (proventriculus), and (4) 'Uebergangstheil' (ventriculus plus post-ventriculus).

De Quatrefages (1865) (**10,** tome ii, p. 3) recognized buccal cavity, and pharyngeal, dentary, and oesophageal regions of the proboscis.

Claparède (1868) distinguished: 'gaine de la trompe' (buccal cavity), 'trompe' (pharynx), 'proventricule', 'ventricule' with its glands (caeca).

Eisig (1881) describes the 'Rüsselösophagus' as made up of three sharply-separated regions—the first (pharynx), the second ('Drüsenmagen'), and the third, which he does not name, but which is the ventriculus: this is followed by

the 'Vormagen' (post-ventriculus) from which the cæca are given off.

Malaquin (1893) designates the divisions 'gaine pharyngienne' (buccal chamber), 'trompe pharyngienne' (pharynx), 'proventricule', and 'ventricule' (ventriculus plus post-ventriculus).

McIntosh (1908) describes the region as consisting of (1) pharyngeal cavity, (2) protrusible proboscis, (3) proventriculus, followed by (4) a short portion which ends in a dilated region often with two lateral cæca (see Pl. 15, fig. 6).

II. The Buccal Chamber.

This is the only part which becomes actually evoluted when the proboscis is protruded. It is a short chamber with a cuticle thinner than that of the outer surface: its wall in the ordinary retracted condition is thrown into a number of folds.

III. The Pharynx.

The pharynx is a cylindrical tube, usually of considerable length, straight in the majority, sinuous or coiled in the Autolytidae and in Amblyosyllis. It has a greatly thickened cuticle, the thickened lining terminating abruptly in front in an entire, lobed, or denticulate edge. In front of this is a circlet of papillæ on the surface of which open the numerous fine ducts of the pharyngeal glands. In most cases the pharynx contains a single triangular tooth (or rather stylet) with the base embedded in its dorsal wall. This is nearly always situated at the anterior end, and is so placed that, when the proboscis is protruded, its apex projects freely in front. In some cases the single tooth is replaced by a paired crescentic group of several teeth (Odontosyllis), or by a circlet (Trypanosyllis, Autolytus).

The cellular layer of the pharynx in the anterior part of its extent is a simple epithelium complicated only by being perforated by the system of splanchnic nerves. Posteriorly it becomes greatly modified by the development of numerous gland-cells, so that it virtually assumes the character of

a gland. In the Exogoneae this gland, which I have termed the anterior proventricular, is more conspicuous than in the other groups of the Syllidea owing to its being more distinctly marked off; but in the latter it is quite as important so far as relative development is concerned (fig. 7). The cuticle in this region is as thick as it is throughout, and appears quite imperforate, so that the secretion of the gland must find its way out elsewhere. As in Exogoneae, in fact, the ducts of the gland-cells run back through the epithelium to the anterior region of the proventriculus, where the cuticle is very thin and, apparently from its staining reactions, not strongly chitinized. Here most of the ducts terminate, though some appear traceable for some distance in the region behind the chitinous plates.

Eisig describes the structure of the pharynx correctly as regards the greater part of its length. The change which takes place at the posterior end he describes rightly as regards the epithelium, but he falls into an error in stating that in this region the structure corresponds closely with that of the ventriculus, not only in the modification of the epithelium, but in the development of radial muscular fibres.

Malaquin gives a more exact account of the structure as far as the Syllidae and Eusyllidae are concerned. He recognizes the glandular modification of the epithelium at the posterior end, but assumes that this has to do with the growth of the pharynx and the formation of additional chitin. In Amblyosyllis and Autolytus, with elongated coiled pharynx, he places the glandular region towards the middle instead of at the posterior end, i.e. instead of at the opening into the proventriculus, where it occurs exactly as in the Syllidae and Exogonae.

In connexion with the pharynx and its papillae mention has been made of the pharyngeal glands, the secretion of which is discharged on the surface of the latter. As I have pointed out (7, p. 229), these glands were referred to by Claparède (2) and De Saint-Joseph (11) and were fully described by Malaquin (9). They consist, in most cases, of about

ten narrow cylindrical bodies of varying length surrounding the pharynx, with which they run parallel, ending blindly behind, and in front terminating in the pharyngeal papillae.

They are solid bodies each of the nature essentially of a group of greatly elongated cells, the anterior end of each of which is produced into a narrow duct terminating in a very minute aperture on the surface of the corresponding papilla.

In Odontosyllis the arrangement of these glands is, as pointed out by Malaquin, somewhat modified by their restriction to the ventral side. In Amblyosyllis and in certain species of Autolytus, as also observed by Malaquin, they are fused together into a pair of irregular masses of considerable size. These divide up in front into narrow lobes running forwards to the papillae.

IV. The Proventriculus: General Structure.

The proventriculus is an exceedingly conspicuous and very characteristic structure to which reference is made by all writers who have dealt with this group of the Polychaeta. But it was not till, in 1881, Eisig published his paper entitled 'Ueber das Vorkommen eines schwimmblasenähnlichen Organs bei Anneliden' that an approximately correct interpretation was given of the structure of this complex organ.

In Eisig's account, though it marks a distinct advance in our knowledge, there are certain omissions and certain misstatements. Of the former one of the most important is the failure to recognize that the muscular tissue of the radial columns, which make up the bulk of the substance of the wall of the organ, is of the striated type. The true nature of this tissue was pointed out by the present writer in a short paper published in this journal in 1886; and the subject, as regards the histology of the muscular tissue, was further developed in 1889 (**6**).

In 1893 was published Malaquin's 'Recherches sur les Syllidiens'. In this comprehensive work the author gives a very full account of the proventriculus, summarizing previously published results and adding numerous observations

of his own. He gives many details, more especially regarding the radial columns of striated muscle and the variations which they undergo in different families and genera. Since the publication of Malaquin's valuable work there has not, so far as I am aware, been any further contribution to the subject with the exception of the brief reference to it contained in a paper on the Exogoneae contributed by me to the Linnean Society (7).

On approaching this subject anew, with a wider command of material, I have found that Malaquin's account, excellent though it is, with many new observations, is yet not altogether correct in some respects, and leaves untouched several structural features that seem to be of some importance in connexion with the study of the proboscis as a mechanical system.

The proventriculus is of cylindrical or sub-cylindrical form, usually with a small degree of lateral compression, and varies greatly in length in different members of the group. The surface is marked by a series of rings, an appearance which examination with a low power of the microscope shows to be due to the presence of annular fine lines and rows of dots. The fine lines correspond to annular bands of non-striated muscular fibres: the dots, which are frequently coloured in the living animal, are the outer ends of the cores of the radial columns of striated muscle. Along the dorsal side of the organ runs a longitudinal light or coloured line, the dorsal raphe, and a similar ventral raphe runs along the ventral side.

A comparison of the pattern on the surface of the proventriculus in representatives of different groups of the Syllidea reveals the occurrence of three main types. In one of these the annular lines alternate with the rows of dots. In a second the lines run through the dots. In the third type, which is the prevalent one in the Syllidae and in the Exogoneae, while the lines perforate the dots in all the lateral regions, they leave that position in the neighbourhood of the raphes, and pass to the latter in the intervals between the rows of dots.

These three types of pattern arrangement mean respectively :

(1) that the annular bands run throughout in the intervals between the radial muscle-columns; (2) that the annular bands perforate the muscle-columns throughout; and (3) that the same arrangement as in (2) holds good except in the neighbourhood of the raphes, where the annular rings pass to the position they occupy throughout in (1).[1]

The lumen of the proventriculus may be described as a vertical slit the upper and lower ends of which lie near the dorsal and ventral raphes respectively. This is the form assumed in the contracted state; in complete contraction the sides of the slit are in close contact: when dilated the slit expands till in transverse section its outline becomes ellipsoidal.

The thick wall of the proventriculus (Pl. 15, fig. 1) consists of the following layers: (1) splanchnic layer of coelomic epithelium: (2) outer fibrous membrane; (3) layer of radial muscle-columns and annular muscle-bands; (4) inner fibrous membrane; (5) enteric epithelium; (6) cuticle.

The coelomic layer is a very thin one, recognizable by its infrequent flattened nuclei. The outer fibrous membrane is the layer described by Malaquin, and earlier by myself, as a layer of non-striated muscle. Of its contractile character I am by no means certain. It is a thin layer, only about 0·003 mm. in thickness in the largest forms, and is made up of two strata in the outer of which the fibres run transversely and in the inner longitudinally: the fibres are exceedingly fine and there are no nuclei. The chief function of this layer seems to be to serve for the insertion of the radial fibres and the fibres of the annular bands. The inner fibrous membrane is a similar layer, also composed of outer transverse and inner longitudinal fibres: it has the inner ends of the radial fibres inserted into it. At the raphes paired trabeculae pass at regular intervals from the inner fibrous membrane to the outer and bind the two layers firmly together.

The enteric epithelium and the cuticle need not be specially

[1] Towards the anterior end of the proventriculus the regularity of the rings on the surface is broken owing to a modification in the arrangement of the radial muscles associated with the presence of the chitinous plates.

described here. They both become specially modified towards the anterior end of the organ in connexion with the valvular apparatus to be described later.

V. The Proventriculus: Muscular Elements.

The greater part of the substance of the thick wall of the proventriculus (figs. 1–5) is made up of the radial muscle-columns and the annular bands. The former are hollow fibres, squarish or polygonal in cross-section, arranged in annular rows, and extending radially from the outer fibrous membrane to the inner.

The hollow of each column is occupied by a protoplasmic core. In the columns which are perforated by the annular bundles the protoplasm is divided into anterior and posterior halves, and this division may extend to the inner end, but not to the short portion of the core outside the annular bands, the two halves being here continuous. In the Exogoneae and in certain members of the other groups each core contains only a single nucleus. But in the rest the structure is more complicated and the number of nuclei increased. The maximum of complexity is reached in the case of Syllis coruscans. In this species (fig. 4), in which the arrangement of the muscles is of type 2, the core is permeated by a system of exceedingly fine fibrils—forming an irregular meshwork with a prevailing longitudinal arrangement: this is more condensed towards the outer end. Communications occur between adjoining cores of the same row along the lines of the annular bands, and there are also communications, irregularly arranged, between the columns of neighbouring rows by means of processes which perforate the cortex. Fibrils from the meshwork of each core radiate outwards and penetrate through fissures into the substance of the cortex. Such communications are most numerous opposite the Z membranes (Krause's membranes) of the cortex, if they are not entirely restricted to such an arrangement.

Nuclei are present in large numbers in each core. These are of two main varieties—larger, clearer nuclei of about 0·0075 mm. in diameter, and smaller, denser, of a diameter of

about 0·005 mm. The former are less numerous, mainly situated towards the outer end, but occurring throughout the core to its inner extremity. The smaller nuclei are extremely numerous, distributed fairly uniformly throughout the length of the core. In addition there are a comparatively small number of nuclei belonging to what appear to be distinct cell-elements with fine-grained cytoplasm embedded in the core. Surrounding the cortex is a layer continuous with the core at the longitudinal fissure, composed apparently of similar material, and containing an occasional nucleus: the investments of contiguous columns coalesce completely.

Slightly less complex than Syllis coruscans are the cores in Trypanosyllis zebra. In this species the arrangement of the muscles conforms to type (3). The cores here consist of two kinds of material—an axial part, split into two in the perforated fibres, and a peripheral part. The former is loaded with rounded granules which are strongly coloured by haematoxylin; the latter appears as a meshwork of delicate threads, prolongations of which pass into the substance of the cortex. Strands of granules similar to those in the central part of the core run longitudinally between the fibrils of the cortex, and the latter is enclosed in an investing layer which encloses similar granules. The central part of the core contains numerous nuclei.

In Syllis variegata (figs. 2 and 3), in which also the arrangement of the muscles conform to the third type, the core is greatly simplified. In the perforated columns it is split longitudinally into anterior and posterior halves which unite together only at the extreme outer ends outside the annular bands. The substance of the core and the layer investing the cortex is a finely granular homogeneous material which does not become very readily stained. In this are embedded some five or six nuclei, one (or two) of which are larger than the others (about 0·008 to 0·01 mm. in long diameter), and are situated usually about the middle of the length of the fibre, while the rest are mostly towards the outer end. The core has a thin investment of what looks like fibrillated material.

As regards the cortex of the column. This consists of a bundle of fibrils among which penetrate branching processes from the protoplasmic core. Each column or fibre is characterized, except in the Exogoneae, by the presence of one (Typosyllis variegata, T. closterobranchia, T. truncata), or more 'striations'. In all essentials these fibres resemble the striated fibres of Arthropods and Vertebrates. The fibrils of each are bound together by one or more transverse membranes (Krause's membranes, telophragms) which pass through the fibrils, and, through the interfibrillar substance, bind all the fibrils intimately together. The fibre itself is composed of alternating zones of singly and doubly refracting material, the telophragms passing through the latter. Moreover, gold-chloride methods reveal systems of J-granules (sarcosomes) and transverse networks in the neighbourhood of the telophragms, exactly as is the case in the striated muscles of Arthropods and Vertebrates.[1]

At their outer and inner ends the fibrils of the striated muscular fibres are firmly fixed into the outer and inner fibrous membranes.

Occupying much less bulk than the radial fibres are the annular bundles of non-striated fibres. The extent of this system, its relations and the part which it plays in the movements of the proventriculus, have not hitherto received adequate attention. Malaquin, a little misled by his idea of a system of transverse septa separating the annular rows of muscle-columns from one another, pays little heed to these bundles. He says in his account of the proventriculus of the Autolytea (p. 217), 'Comme nous aurons l'occasion de le voir plus loin pour d'autres types, il est des points du diaphragme où les fibrilles, s'arrangeant en faisceaux, ont tout à fait l'apparence de fibres musculaires, et on peut croire alors que ce tissu conjonctif fibrillaire passe au tissu musculaire proprement dit. Nous reviendrons sur ce point à propos d'un autre type'.

[1] Mesophragms and Q-granules I have not hitherto succeeded in detecting, except somewhat doubtfully in the case of Syllis (Typosyllis) variegata.

The only further mention is under Syllis hyalina (p. 227) : ' Les diaphragmes transversaux ont la même disposition et la même structure, à part ce fait que le tissu fibrillaire qui les compose présente vers la périphérie un arrangement en faisceau très marqué.'

But these annular muscles, as they may be termed, are of much greater importance than such casual mention as that given above would imply.

Each annular muscle is a bundle of non-striated fibres, compressed in the antero-posterior direction, running (in the prevailing third type) transversely between two adjoining rows of radial striated fibres in the immediate neighbourhood of the raphes, and, farther on, passing through the outer ends of the radial fibres. At the raphe the annular muscle is continued straight across the middle line to the opposite side. From the raphe the muscle runs in an annular way in the position indicated above, and is inserted at intervals into the outer fibrous membrane. These insertions occur between the radial fibres of the row, around the corresponding accessory fibres (non-striated radial fibres) described below.

It will thus be seen that the annular muscles are so arranged as to form a system of constrictors by means of which the lumen of the proventriculus, dilated by the action of the radial fibres, is contracted.

The striated fibres, though the most important, are not the only radial fibres in the wall of the organ. Another set of radial elements, hitherto entirely overlooked, play a part which must be of some consequence, since their occurrence seems to be universal, and their arrangement varies little. These elements, which for the sake of distinction may be called the accessory or non-striated radial fibres, like the striated, run from the outer fibrous membrane to the inner. They are single fibres (usually bifurcated close to the outer end in S. variegata, usually branched in S. coruscans), placed at regular intervals between the striated fibres, as shown in figs. 1 to 4. As mentioned above, the main relations of these fibres are with the annular strands of non-striated

muscle, and their chief function would seem to be to provide a series of 'points d'appui' for the latter. It may be mentioned here that it is largely to the presence of these fibres in transverse sections in certain planes that the illusion of regular partitions between the rows of striated fibres is due.

VI. The Proventriculus: Chitinous Plates.

In the interior of the proventriculus towards its anterior end is an elaborate structure which has hitherto failed to receive the notice which its importance in the mechanism of the proboscis seems to demand. It occurs in essentially the same form in all the members of the group which I have examined for it—not only in the Syllidae and Eusyllidae, but in the Exogoneae and Autolytidae.

De Saint-Joseph seems to have been the first to direct attention to the appearance presented by this structure, though he misunderstood its significance. In his description of Typosyllis alternosetosa, he says, 'le proventricule, avec 30 rangées de points gris, qui a à sa partie supérieure un anneau chitineux', with a foot-note, 'Cet anneau, qui se remarque souvent chez les Syllidiens, me paraît être la continuation de la trompe qui pénètre dans le proventricule'. On the other hand, he refers to the same structure in Pterosyllis spectabilis as 'deux valves cornées' (pp. 65 or 189). Malaquin (p. 213) gives a much more consistent and complete description: 'Dans la région antérieure de l'organe, l'épithélium prend un autre aspect, il devient en quelque sorte fibrillaire; les cellules en sont très allongées avec noyau médian (Pl. v, fig. 7, *Ep. pr.*). Cette structure correspond à une disposition particulière, à un épaississement de la cuticule formant en avant du proventricule un anneau chitineux. Cet anneau chitineux, visible sur le vivant (Pl. iv, A. *ch.*, figs. 1, 2, 3, 4, 5), peut surtout s'étudier dans une coupe horizontale du proventricule (Pl. v, fig. 6). Dans la région antérieure de l'organe l'épithélium est beaucoup plus épais et les parois se touchent à l'état de repos de manière à fermer totalement la lumière.

En arrière de cet épaississement existe l'anneau chitineux auquel correspond une disposition particulière des colonnes musculaires : celles-ci, au lieu d'être régulièrement radiaires, sont obliquement disposées, au moins dans le plan horizontal médian du proventricule, de façon à agir dans deux sens perpendiculaires. Cette disposition est destinée probablement à faire glisser et au besoin à comprimer fortement les aliments avalés par l'animal.'

A short distance behind the abrupt posterior edge of the thickened cuticle of the pharynx (fig. 5) is a deep transverse (circular) groove in the thick epithelium, and a little farther back a second similar groove, the two separated from one another by a prominent band of thickened epithelium. Just behind the posterior groove the cuticle is developed on either side into a dense chitinous plate. These plates are of no great length in the direction of the long axis of the body, but considerably elongated vertically, extending downwards so as to bound almost the whole of the slit-like lumen (Pl. 15, fig. 1). At the dorsal and ventral edges of each run grooves in the epithelium. Dorsally and ventrally these plates pass into the unmodified cuticle which bounds the lumen of all the rest of the organ : anteriorly the same holds good, but posteriorly each plate projects a little beyond the general level of the surface, as the free edge of a finger-nail, elsewhere lying close on its bed, projects beyond the general surface of the digit. The radial muscle-columns of the wall of the proventriculus in the belt through which these chitinous plates extend, depart from their arrangement in regular annular zones (fig. 5), and, as observed by Malaquin, run obliquely inwards and forwards or inwards and backwards. The object of this oblique direction would seem to be to enable the two plates to be tilted up so that their edges may be brought into contact.

VII. The Ventriculus.

The ventriculus is a small chamber, reduced or absent in some. It has fairly thick walls with a correspondingly reduced lumen. Numerous thin bundles of muscular fibres run radially

through the substance of the wall ; but the chief space is taken up by the epithelium modified into a mass of gland-cells similar to those composing the anterior proventricular glands. They are apparently syncytial, and in most specimens present the appearance, in the aggregate, of a mass of sinuous and anastomosing tubules and vacuoles with thin walls and without distinct contents : more rarely the spaces are filled with a secretion capable of taking a strong stain with haematoxylin. In the Exogoneae the ' ducts ' from this mass of unicellular glands do not seem to open—in great number at least—into the cavity of the ventriculus itself, but run forwards to open into the recess at the extreme posterior end of the proventriculus. It is in very few preparations that this destination is traceable : the specimen must happen to have been fixed when the secretion was actually being discharged, and the strands of secretion by which alone the course of the ' ducts ' is traceable, must have become differentially stained. In the other sections of the Syllidea I have not been able to trace this connexion, and I am led to conclude it is not universal.

VIII. The Post-ventriculus.

Sharply marked off both from the ventriculus in front and the intestine behind is the chamber from which are given off laterally the two caeca present in most of the Syllidea with the exception of the Autolytea.

This, as already noticed, is recognized as a separate chamber by Eisig, and he gives prominence to it as the second main division of the alimentary canal—the first being the whole proboscis-oesophagus (Rüsselösophagus) and the third the intestine. De Saint-Joseph, on the other hand, and Malaquin do not recognize the distinctness of this chamber from the proventriculus. Its walls have only a thin layer of muscle [1] without radial fibres. Its epithelium is ciliated and is loaded

[1] It may be pointed out here that Malaquin was in error in stating that the intestine is devoid of a muscular layer. There is a thin layer of flattened fibres, not placed in close contact with one another, composed of outer longitudinal and inner circular elements.

with unicellular glands. The caeca are of essentially the same structure, with numerous unicellular glands which discharge their secretion into the lumina. A name is needed to designate the small but distinct part of the digestive canal from which the caeca are given off. The term oesophagus is in general use for a corresponding part in the Nereids; but, whatever its claims, it seems inappropriate to a compact glandular chamber with a ciliated epithelium. I propose instead the term post-ventriculus as not involving any doubtful homologies and indicating simply position.

Though the post-ventriculus, with the caeca, resembles the intestine in its ciliated epithelium, it differs from the latter in the presence of the very numerous and characteristic unicellular glands. It is also sharply constricted off from it, and the narrow aperture of communication between the two is guarded by a valve composed of folds of the intestinal epithelium which must prevent the passage of liquid forwards from the intestine.

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EXPLANATION OF PLATE 15.

Lettering common to all Figures.

am., annular bands of non-striated muscle; *a.pr.g.*, anterior proventricular glands; *a.r.*, accessory radial fibres; *c.p.*, chitinous plates of proventriculus; *cu.*, cuticle; *e.m.*, external membrane; *ep.*, epithelium; *i.*, intestine; *i.m.*, internal membrane; *p.*, pharynx; *pa.*, pharyngeal papillae; *p.g.*, pharyngeal gland; *pr.v.*, proventriculus; *pt.*, post-ventriculus; *r.*, radial muscle-columns.

Fig. 1.—Diagram of a transverse section of the proventriculus of Syllis: about one quadrant shown. The section is represented as passing through the chitinous plates; but the typical arrangement of the muscles is illustrated—not the modified arrangement in the chitinous plate region (see fig. 5). The coelomic epithelial layer is not represented in this or the other figures.

Fig. 2.—Part of a transverse section of the proventriculus of Syllis variegata (Grube). ×330. The dark transverse lines passing across the radial muscle-columns indicate the telophragms. The accessory radial (*a.r.*) fibres are drawn in black, as in the other figures, for the sake of contrast.

Fig. 3.—Portion of a tangential section of the proventriculus of S. variegata internal to the annular bands. ×330. The pattern of the transverse sections of the cortex ('Cohnheim's areas') is not represented in this or in the following figure.

Fig. 4.—Portion of a tangential section of the proventriculus of S. coruscans (Haswell), internal to the annular bands. ×330.

Fig. 5.—Part of a horizontal section of the proventriculus of Syllis closterobranchia (Schmarda), passing through the chitinous plates. ×330.

Fig. 6.—Diagrammatic general view of the proboscis of a Syllis from above: part of the dorsal wall of the pharynx and proventriculus removed to show the region of the anterior proventricular glands and the chitinous plates. Only one of the pharyngeal glands is represented. *a.pr.g.*, anterior proventricular glands; *c.*, caeca; *c.p.*, chitinous plates; *cu.*, thickened cuticle of the pharynx; *i.*, intestine; *p.*, pharynx; *pa.*, pharyngeal papillae; *p.g.*, pharyngeal gland; *pr.v.*, proventriculus; *pt.*, post-ventriculus.

Fig. 7.—Semi-diagrammatic view of a horizontal section through the junction of the pharynx and proventriculus of Grubea to show the position and relations of the anterior proventricular glands. ×780.